

## Validation of age determination using otoliths of the European anchovy (*Engraulis encrasicolus* L.) in the Bay of Biscay

A. Uriarte<sup>A,D</sup>, I. Rico<sup>A</sup>, B. Villamor<sup>B</sup>, E. Duhamel<sup>C</sup>, C. Dueñas<sup>B</sup>,  
N. Aldanondo<sup>A</sup> and U. Cotano<sup>A</sup>

<sup>A</sup>AZTI Tecnalia, Marine Research Division, Herrera Kaia Portualdea z/g, E-20110 Pasaia, Spain.

<sup>B</sup>Instituto Español de Oceanografía (IEO), Promontorio de San Martín s/n, E-39080 Santander, Cantabria, Spain.

<sup>C</sup>Institut Français de Recherche et d'Exploitation de la Mer (IFREMER), Lorient station, 8 rue François Toullec F-56100, Lorient, France.

<sup>D</sup>Corresponding author. Email: [auriarte@azti.es](mailto:auriarte@azti.es)

**Abstract.** Validation of the age determination procedure using otoliths of European anchovy in the Bay of Biscay was achieved by monitoring very strong year-classes in successive spring catches and surveys, as well as the seasonal occurrence of edge types. Historical corroboration of the ageing method was obtained by cross-correlation between successive age groups by year-classes in catches and surveys (1987–2013). Summary annual growth in length is also presented. Yearly annuli consist of a hyaline zone (either single or composite) and a wide opaque zone, disrupted occasionally by some typical checks (mainly at age-0 and age-1 at peak spawning time). Age determination, given a date of capture, requires knowledge of the typical annual growth pattern of otoliths, their seasonal edge formation by ages and the most typical checks. Most opaque growth occurs in summer and is minimal (translucent) in winter. Opaque zone formation begins earlier in younger fish (in spring), and this helps distinguish age-1 from age-2+.

**Additional keywords:** age estimation, checks, Engraulidae, otolith formation.

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### Introduction

Age determination for short-lived fish species by examination of otoliths can be difficult because of the predominance of young fish (0, 1 or 2 year olds), which often show false rings or checks (Melo 1984; Waldron 1994; Waldron and Kerstan 2001; Panfili *et al.* 2002). The assessment of growth and demography of short-lived species in temperate and tropical latitudes often uses length-based methods (Palomares *et al.* 1987; Bellido *et al.* 2000; Cubillos *et al.* 2001). However, insights into the growth dynamics and actual demography gained from the use of otoliths for age determination have led many groups working with short-lived pelagic species to adopt such procedures (Aguayo 1976; Thomas 1983, 1985; Melo 1984; Morales-Nin and Perterra 1990; Hoedt 1992).

Age determination of sardines and anchovies in several areas of the Mediterranean and Atlantic waters is problematic (ICES 2009, 2011; Ameri *et al.* 2011). The European anchovy (*Engraulis encrasicolus* L.) supports an important fishery in the Bay of Biscay (latitude 42–48°N). Anchovy spawning takes place primarily from April to July during the spring warming up of sea surface temperatures (SST) between 13 and 19°C (Motos *et al.* 1996; Petitgas *et al.* 2010). There is a traditional Spanish fishery

that takes place in spring based on purse seining, and a French fishery that occurs primarily during the second half of the year and based mostly on pelagic trawling (Uriarte *et al.* 1996; ICES 2014). Stock assessment relies on direct monitoring by surveys, namely an acoustic survey (Pelgas series; Massé 1996; Massé *et al.* 2016) and a daily egg production method (DEPM) survey (Bioman series; Motos *et al.* 2005; Santos *et al.* 2016). Both surveys supply biomass and population at age estimates in May for the integrated assessment carried out by the ICES (2014), which applies a Bayesian biomass-based model (Ibaibarriaga *et al.* 2011) structured on two age groups: 1 and ≥2 years older age classes (referred to as age-1 and age-2+).

Early studies on the growth of anchovy in the Bay of Biscay had been performed by direct examination of catch by length distributions (Navaz and Lozano 1966; Guerault and Avrilla 1973). However, otolith examination soon became the preferred method (Guerault and Avrilla 1974; Cendrero *et al.* 1981; Astudillo 1986; Junquera 1986). In recent decades, age determination from otolith examinations has followed procedures first applied by Uriarte and Astudillo (1987) and described and agreed through several workshops on anchovy age reading that have occurred since 1990 (reports are available in the repository

of ICES Planning Group on Commercial Catches, Discards and Biological Sampling (PGCCDBS), see <http://www.ices.dk/community/Pages/PGCCDBS-doc-repository.aspx>, accessed 2 January 2016; complete references available in ICES 2009). These reports have assessed the consistency and precision of age determinations. However, the original validation studies supporting this method were not published.

The purpose of this article is to present results of a study of the annual and seasonal growth of otoliths that served to validate age determination from otoliths for the anchovy in the Bay of Biscay, completed by historical corroboration of the age determination method up to the present day and a summary of the annual growth pattern (in length) of this anchovy resulting from it. Supplementary material is available online containing a seasonal description of otoliths by ages and of their marginal edge formation (with pictures; see first section of the Supplementary material), a quantitative analysis of the size of the annual otolith increments by ages (see second section of the Supplementary material) and a summary of the incidence of checks between 1984 and 1991 (see the third section of the Supplementary material).

The method has served to deduce the demography of the catches and of the population estimates from surveys since 1987. It provided the foundations for several studies on spatial distribution of adults at spawning time (Motos et al. 1996; Vaz et al. 2002; Ibaibarriaga et al. 2013) and on the modelling of otolith shape (Gonzalez-Salas and Lenfant 2007) and growth (Hernández et al. 2009, Pecquerie et al. 2009, 2012). Beyond this, recent studies on otolith micro-increment formation of this anchovy have enabled the daily rhythm of deposition to be established in larvae (Aldanondo et al. 2008), as well as in juveniles and adults (Cermeño et al. 2003), and the method for otolith daily increment examination (Cermeño et al. 2008). A validation of the formation of the first annulus for this anchovy is also presented in this special issue by daily increment examination of reared juveniles (Aldanondo et al. 2016).

Materials and methods

Sampling

Age validation was based on otoliths from monthly collections from the Spanish (national and regional) catch sampling programs between 1984 and 1992, taken at random up to 1986 and stratified to size categories from 1987 onwards (Table 1). Some additional samples came from acoustic surveys (SARACUS 1985 (Instituto Español de Oceanografía (IEO), Spain) and

EIGAS 1985 and 1986 (Institut Français de Recherche et d'Exploitation de la Mer (IFREMER), France)). Length distribution and age composition of the Spanish spring fishery between 1983 and 1987 has been reported in Astudillo (1986) and Uriarte and Astudillo (1987), whereas for 1988–92 the data have been published in ICES reports (Anon. 1989, 1991, 1992, 1993). Although no otoliths were available for 1983, for the purposes of the present study we used the rough inference from lengths made by Uriarte and Astudillo (1987). Finally, for 1984, a new age–length key (ALK) was prepared based on the current age determination criteria and applied to the length distribution in Astudillo (1986).

Biological samples consisted of a minimum of 40 fish, taken randomly from the landings, for which total length (TL; mm), weight (g) and sexual maturity was recorded and sagittal otoliths extracted. Otoliths were washed with water and dried for 24 h before setting the entire otolith in transparent resin inside holes made over black plastic slide containers. Both otoliths were laid in parallel with the sulcus facing down.

Age determination procedures

The otoliths were observed under a binocular microscope at a magnification of 20×, applying incident double oblique light (from both sides) as recommended in ICES (2009). The basic information required for age determination is the date of capture. Knowledge of individual fish length is not required. For this anchovy, conventional birthdate is set at 1 January. Very doubtful age determinations were discarded from posterior processing if not agreed after a second examination by two readers.

Age determination is based on knowledge of the annual growth pattern of anchovy otoliths, seasonal growth of the edge (by ages) and of the most typical checks. The ageing criteria agreed in the 2002 workshop (Uriarte et al. 2002), following the original validation, are listed below.

1. Number of complete annual growth zones (annuli): the assigned age equals the number of complete opaque growth zones corresponding to the expected annual growth pattern of the otoliths, excluding the marginal edge development of the year. The translucent zones are usually formed in winter, but are not necessarily present from the beginning of the year. Typically, successive annual opaque growth zones are expected to be of decreasing width (Morales-Nin and Panfili 2002). Where the number of opaque zones does not correspond to the typical expected annual growth pattern for

Table 1. Monthly collection of otoliths by ages and samples (bottom row) available for the analysis of the occurrence of edge types throughout the year from 1984 to 1992

Ages	Months												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Age 0	0	0	0	0	0	0	0	1	95	259	327	78	760
Age 1	87	0	435	541	1048	908	308	177	242	6	16	6	3774
Age 2	6	0	205	483	805	375	132	61	25	5	11	0	2108
Age 3+	0	0	149	271	266	116	69	1	17	0	2	0	891
Total otoliths	93	0	789	1295	2119	1399	509	240	379	270	356	84	7533
Samples	3	0	22	40	64	40	17	11	12	9	12	3	233

the presumed age, the existence of false increments (checks) can be suspected.

2. Conformity of marginal edge development with the expected type of edge at the month of capture for the presumed age: if the edge does not match the expectation, then alternative interpretations could be considered, including the potential occurrence of checks.

This anchovy can lay down several typical checks (mainly during age-0 and age-1) and it is important to recognise these for correct age determination. These checks are easily recognised in old fish, for which annual growth patterns are well established and age determination is easy. The checks are usually faint translucent zones, clearly visible but of less intensity than true winter translucent zones placed within the typical annual opaque growth of otoliths. The checks do not always form a complete zone around the otolith.

Checks have been typified and are named with a 'C' plus two digits according to the age of the fish when formed (first digit) and to the approximate relative position over the expected annual growth of the otolith at that age (second digit). For example, the most typical checks formed during the first year of life (age-0) are termed 'C05' or 'C08' because they are formed at ~50 or ~80% respectively of the expected annual growth of the otolith at age-0. Other typical checks are 'C12', 'C15' or 'C18', which correspond to checks formed at age-1 at ~20, 50 or 80% respectively of the expected annual growth of the otolith for that age. The formation of checks C12/15 was studied along with evaluation of edge formation for age-1, noting the time of year when those checks were already recognisable.

The age compositions of catches were obtained by applying the respective ALK to the length distribution, usually on a half-yearly basis (but occasionally quarterly). Usually, more than 1000 age determinations support every ALK, along with considerable sampling for length distribution (ICES 2014), well above the minimum standard sampling requirement established in the European Union Community programme for the collection of data in the Fisheries sector (see [https://datacollection.jrc.ec.europa.eu/c/document\\_library/get\\_file?uuid=296dffd3-9c81-4759-b691-9b1654ea66b9&groupId=10213](https://datacollection.jrc.ec.europa.eu/c/document_library/get_file?uuid=296dffd3-9c81-4759-b691-9b1654ea66b9&groupId=10213), accessed 2 January 2016). For the surveys, spatial explicit ALKs were applied to length distribution of the population estimates of the respective spatial strata (Boyra *et al.* 2013; Massé *et al.* 2016; Santos *et al.* 2016).

#### Age validations

The age determination method and otolith growth pattern were established through three complementary validation studies.

First, the annual growth pattern of otoliths (or annuli identification) was achieved by establishing the correspondence between the types of otoliths and ages in spring through the following two indirect methods (*sensu* Panfili *et al.* 2002):

1. Monitoring of the progression of strong year-classes in the catches over several years (correspondence of successive modal lengths with modal otolith types), which is a well-suited indirect method for short-lived species and for the first age groups of other species (Holden and Raitt 1974; Campana 2001). This was applied to the progression of the 1982 year class in the Spanish spring purse seine fishery between 1983

and 1986 (up to age-4, which was also seen as age-5 in 1987) and for the 1989 year class in the Spanish fishery throughout the year (between 1989 and 1991 up to age-2).

2. Verifying the consistency between sharp spawning biomass fluctuations recorded in the spring DEPM surveys 1987–92 and fluctuations in the biomass of the (presumed) 1-year-old recruits, which validates absolute correspondence between Type I otoliths and the age-1 group. This relies on the fact that for a fish fully mature at age-1 (like this anchovy; Motos 1996), if the survey's observations are rather precise, any sharp increase in the spawning biomass has to be due to a major increase in the 1-year-old recruits.

Second, the seasonal growth pattern of otoliths was established by following the seasonal formation of the otolith margin edge throughout the year using the following semidirect qualitative validation method (Panfili *et al.* 2002):

3. Monitoring of the occurrence of edge types throughout the year by age classes validates the yearly rhythm of annuli formation, improves the understanding of the growth pattern of otoliths throughout the year and completes the age determination criteria in terms of the expected seasonal otolith edge type by ages. We basically followed the nomenclature for the edge types in otoliths adopted by the International Commission for the Southeast Atlantic fisheries (ICSEAF) for hake (ICSEAF 1983; which originated from Jensen 1965) by naming the narrow (N) and wide (W) hyaline-translucent (H) or opaque (O) edges as HN, HW, ON and OW respectively.

#### Historical corroboration of the age determination method

Finally, a set of corroborative indirect validation methods was applied to all available historical age composition of catches and population estimates from surveys (between 1987 and 2013), as reported to ICES (2014) by the Spanish and French Fishery Institutes (applying the current age determination procedures):

1. Checking correlation between the abundance of successive age groups of the same year classes either in catches or in population estimates from surveys. Significant correlations are demonstrative of coherent correlative age estimations (Panfili *et al.* 2002)
2. Checking the consistency between the yearly biomass fluctuations in surveys and changes in percentages of 1-year-old recruits in the respective population estimates, which is a generalisation of the second validation method detailed above. This was tested by applying the following model, which relates the ratio of biomasses in two consecutive years of a survey series to the ratio of age-1 proportions over older fish in the second year (the odds ratio for age-1; Uriarte 2015):

$$\frac{P_{1,y+1}}{(1 - P_{1,y+1})} = \frac{B_{1+,y+1}}{B_{1+,y}} \cdot e^{-g_{1+}} - 1 \quad (1)$$

where  $B_{1+,y}$  and  $B_{1+,y+1}$  refer to the total biomass (all ages) in years  $y$  and  $y+1$ ,  $P_{1+,y+1}$  refer to the percentage in mass of the age-1 group over the total biomass in the second year ( $y+1$ ), and  $g_{1+}$  is the instantaneous rate of biomass decay/increase of all ages pooled together ( $g_{1+} = G_{1+} - M_{1+} - F_{1+}$ ,

- with  $G_{1+}$ ,  $F_{1+}$  and  $M_{1+}$  corresponding to the rates (equal for all ages) of individual growth in mass, natural mortality and fishing mortality respectively). As such, this is a linear model with an intercept of  $-1$  (offset) and a slope (parameter) equal to the inverse of the average survival in biomass of a population from year to year ( $\exp(-g_{1+})$ ). Because  $G$ ,  $M$  and  $F$  usually vary across ages and may change along the time series, the slope cannot properly be considered a constant, but is subject to structural and process error. Although if such variability turns out to be of little magnitude, finding a significant fitting to such relationship should be indicative of an overall satisfactory performance of the age determination, as well as of the biomass estimation procedures of the surveys. This is a suitable model for anchovy because the population mostly consists of two age groups; the 1- and 2+-year-old fish (Ibaibarriaga et al. 2008).
3. Checking the correlation between the juvenile (age-0) estimates in an autumn acoustic survey series started in 2003 (JUVENA; Boyra et al. 2013), with the age-1 recruit estimates in the spring surveys (both DEPM and acoustic) of the following year. This served to verify that juveniles (0 group in autumn) and recruits at age-1 (1 year old in spring) are correctly identified from otoliths.

#### Annual growth pattern in length and growth parameters

Annual growth in length has been studied using the mean length at ages in the Spanish spring fishery 1985–2013, and from the mean lengths at ages in the population obtained from the spring DEPM survey (1990–2013). The mean length at age class was integrated into the von Bertalanffy growth equation:

$$L_t = L_\infty \left( 1 - e^{(-K(t-t_0))} \right) \quad (2)$$

where  $L_t$  is the mean fish length at age  $t$  and  $L_\infty$ ,  $K$  and  $t_0$  are parameters that determine the shape of the growth curve:  $L_\infty$  is defined as the asymptotic mean length,  $K$  the rate at which the curve approaches the asymptote and  $t_0$  the age at which mean length is zero (Ricker 1975). The von Bertalanffy growth function (VBGF) was fitted by direct minimisation of squared residuals to the former mean lengths in an Excel spreadsheet (Microsoft Office 2010, Microsoft Corporation) between ages 1 and 5 (the latter from a single year). Comparison with the growth of other Engraulidae was based on the mean length at age-1 and age-2, on the von Bertalanffy equation parameters and their combination in Pauly and Munro's (1984) growth performance index ( $\phi'$ ):

$$\phi' = \log(K) + 2 \cdot \log(L_\infty) \quad (3)$$

where  $K$  and  $L_\infty$  are VBGF parameters.

## Results

### Validations

#### Annual growth pattern (annuli)

Fig. 1 shows the series of typical otoliths in spring, ordered by an increasing number of opaque growth zones, labelled as otolith Types I, II, III, IV and V (although the latter was only seen in 1987). The length distribution of the spring Spanish catches between 1983 and 1986 (Fig. 2) showed that there was

an increasing modal length during those years, whereas catches peaked in 1984 and later decreased. This was indicative of a very strong year-class (1982) passing through the fishery being followed by weak year-classes so that the progression in length of the cohort could be tracked year after year. Although in 1983 no collection of otoliths was available, the modal incidence of otolith Types II and III in 1984 and 1985 catches and the maximum incidence of otolith Type IV in the series occurring in 1986 led us to conclude that those otoliths labelled as Type I, II, III and IV corresponded to age-1, -2, -3 and -4 respectively. Finally, in 1987, a new group of otoliths showing an additional opaque growth band (compared with age-4) appeared for the first time in a rather remarkable frequency, which corresponded to age-5 of the 1982 cohort. The progression of modal lengths in the Spanish catches between the autumn of 1989 and the spring of 1991 (Fig. 3) also revealed the passing of a big year-class (1989) and corroborated the former correspondence of otoliths Type I and II with age-1 and age-2 respectively.

The close correspondence between the ups and down of the population between 1987 and 1992, as estimated by the DEPM surveys, and the incidence of otolith Type I (age-1) in those surveys (Fig. 4) provided evidence that Type I otoliths actually corresponded to age-1 and completed the former validation procedure.

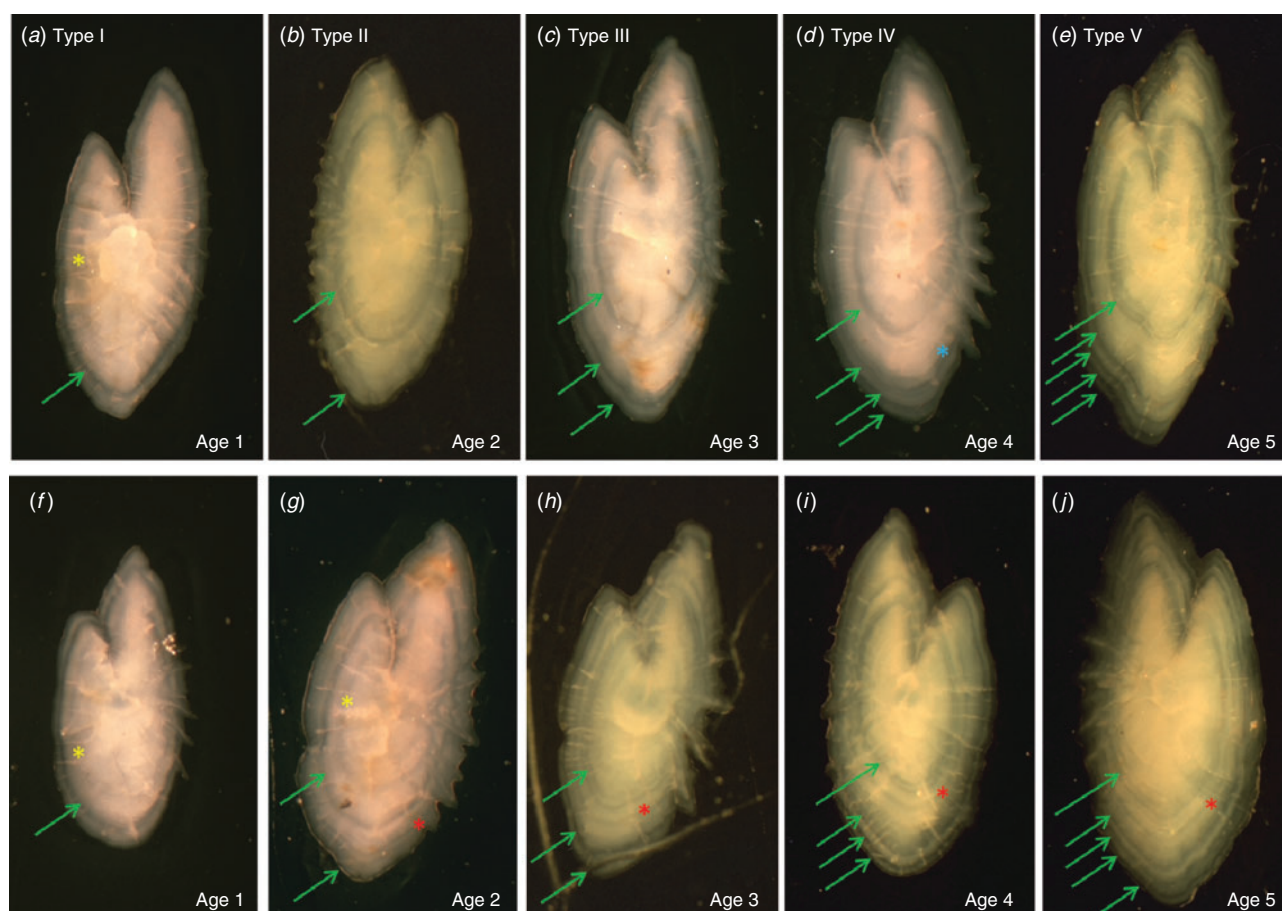
#### Seasonal growth pattern of otoliths by ages

The timing of formation of the opaque edges by age is summarised in Fig. 5. For age-1, growth resumes usually during March, and by April most show marginal opaque growth. However, for the age-2 group, only a few individuals start laying down the marginal opaque growth by May, many do it during June and most have already resumed opaque growth by July. For age-3, it is only in June when some individuals start showing marginal opaque growth, whereas by July most of them will have resumed otolith opaque growth and by August all individuals show opaque edges. So, the older the fish, the later the formation of marginal opaque growth resumes. As such, for age-2 and age-3 (and older), spring is a period when the hyaline zone, laid down in winter, intensifies and becomes more pronounced and wide (HW), whereas for age-1 it is a period of intense growth and formation of an opaque edge.

In addition, we noticed that by September otoliths of all ages show such a wide marginal opaque growth that they seem to have culminated the expected total annual opaque growth.

Further detailed seasonal description of the otoliths by ages (with pictures) and of their monthly margin edge formation is available in the first section of the Supplementary material. Overall, the extent of otolith growth during the first year of life (as age-0, until the first winter translucent zone) is vast and usually accounts for the major part of the otoliths (even for the oldest fish). Otolith growth at age-1 and age-2 diminishes to approximately one-half and one-third of that at the previous age respectively, whereas at older ages the reduction of the annual increments slows down, leading to a gradual (less intense) narrowing of subsequent increments (Fig. 1). The variability around this pattern is large (see a quantitative analysis of otolith growth in the second section of the Supplementary material).





**Fig. 1.** Pictures of anchovy otoliths. (a–e) Images of typical otoliths (Types I–V) found in spring (May) with increasing numbers of white opaque growth zones: (a) Type I (age-1; catch date 29 May 1990); (b) Type II (age-2; 31 May 1985); (c) Type III (age-3; 23 May 1985); (d) Type IV (age-4; 15 May 1986); and (e) Type V (age-5; 6 May 1987). (f–j) Images of otoliths showing the most typical checks. (f) Age-1 showing check C08 (05 July 1990); (g) age-2 showing C08 and C12/15 (22 May 1991); (h) age-3 showing a double first hyaline zone (split ring) and C12/15 (11 April 1985); (i) age-4 showing a double first hyaline zone (split ring) and C12/15 (22 May 1986); and (j) age-5 showing C12/15 (22 April 87). Arrows indicate successive winter hyaline zones; different coloured stars indicated different checks: yellow, C08; red, C12/15; blue, C18. Scale: the area of the images is  $2447 \times 4344 \mu\text{m}$ .

### Checks

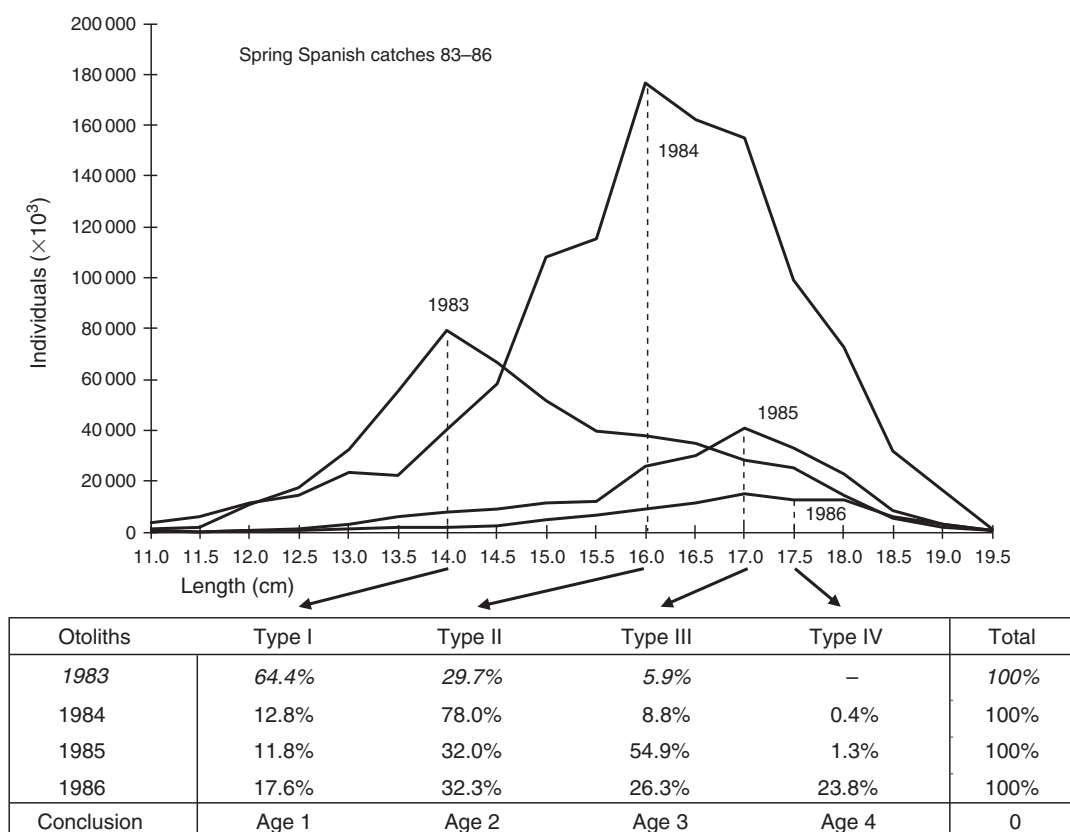
The most typical checks are C05, C08, C12, C15 and C18 (Fig. 1). Checks at age-2 (e.g. checks C22 or C25) are very rare. Not all otoliths have checks and their incidence can change considerably between years. The most frequent checks occur at age-1 (C12–C15), with an incidence ranging between 15 and 60% depending on year-class (see the varying incidence of most typical checks in the period 1984–1991 in the third section of the Supplementary material). We noticed that the presence of C12/15 in the otoliths of the 1-year-old fish increases from mid-year to autumn (from ~10% in June to ~30–40% in July–September). The semihyaline edges that are rather common for the age-1 fish in June–July (Fig. 5) should correspond to the formation of this check.

### Historical corroboration of the age determination method

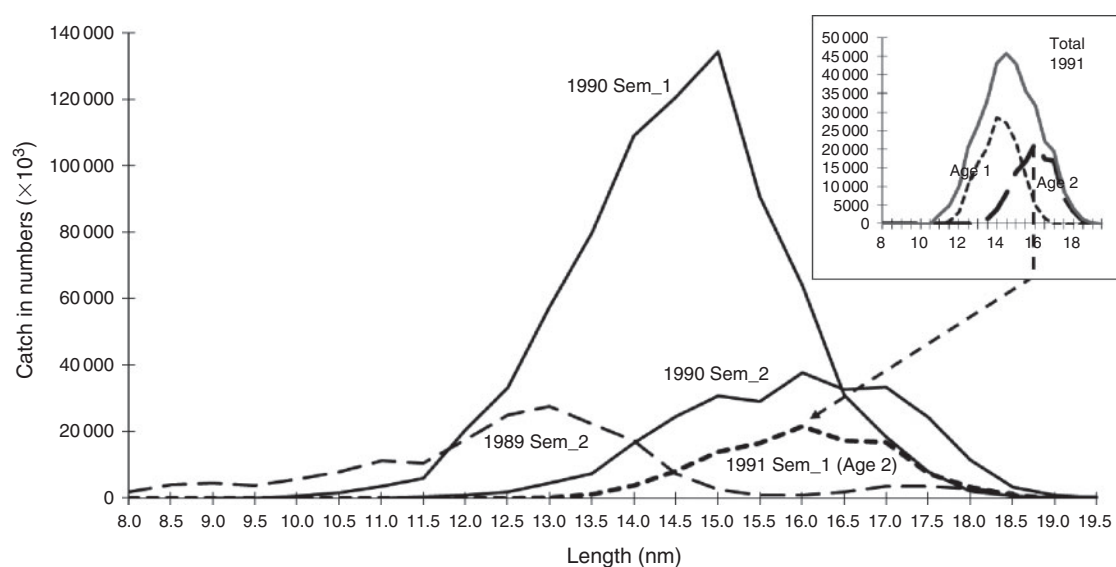
Using the current ageing method to infer the age composition of catches in the period 1987–2013 resulted in a significant correlation of successive catches at age by year-class in the

international fishery (Fig. 6). This is indirect validation of the otolith age determination method because ages have to be determined rather precisely for it to be true. Parallel analysis of the national fisheries reveals that the French catches at age show significant relationships for all ages throughout the entire time series (with  $r = 0.829$  ( $P = 1 \times 10^{-5}$ ) and  $r = 0.555$  ( $P = 0.011$ ) for ages-1–2 and ages-2–3 respectively). For the Spanish spring fishery, the correlations were also significant up to the closure in 2005 (with  $r = 0.489$  ( $P = 0.046$ ) and  $r = 0.657$  ( $P = 0.004$ ) for ages-1–2 and ages-2–3 respectively), but the addition of the years after the reopening of the fishery (2010–13) rendered the relationship between age-1 and age-2 not significant ( $P = 0.160$ ) because of the unusually large quantity of catches of age-2 over age-1 compared with previous years; however, the relationship between age-2 and age-3 remained significant ( $P = 0.013$ ).

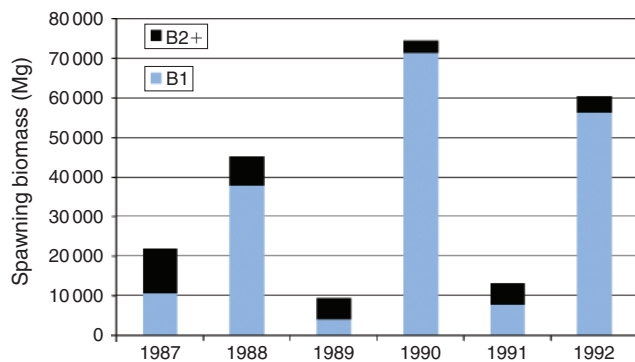
The same analysis for surveys shows significant correlation of successive age groups by year-class of the populations at age estimates (at an  $\alpha$  of 10%, not always at 5%). For brevity, no graphs are shown, but correlations between successive population estimates at age-1 and age-2, as well as age-2 and age-3 for the



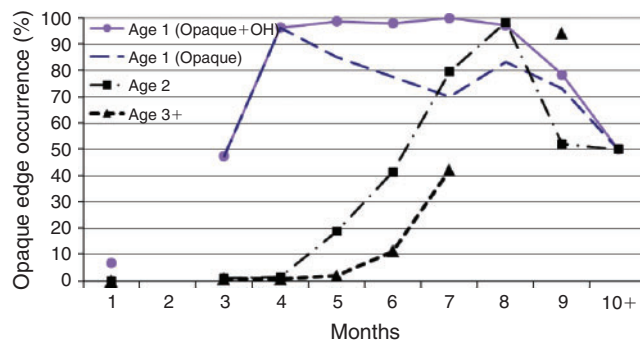
**Fig. 2.** Length distribution of the spring Spanish catches from 1983 to 1986 and corresponding percentages of the different otolith types (Types I–IV) in the catches, which themselves correspond to the age groups 1–4 respectively. In the inset table, for the 1983 Type IV data there was no biological sampling and proportions by ages were inferred from length distributions (Uriarte and Astudillo 1987) with a 3+. Adapted from Uriarte and Astudillo (1987) and Uriarte *et al.* (1996).



**Fig. 3.** Progression of the length distribution of the 1989 cohort up to age-2, as reflected in the Spanish catches from the second half of 1989 to the first half of 1991, on a half-yearly basis. For the first half of 1991, only the length distribution corresponding to age-2 is shown as subtracted from the total length distribution. The inset shows the spring Spanish catches at length and by age in 1991, from which the length at age-2 distribution was used for the main graph (arrow). Sem\_1, refers to first half of the year; Sem\_2, refers to the second half of the year.



**Fig. 4.** Spawning biomass fluctuations 1987–92 (daily egg production method (DEPM) surveys; ICES 2014) and corresponding biomass by age-1 (B1) and age-2+ (B2+).



**Fig. 5.** Occurrence of marginal opaque edges (adding up the opaque narrow and wide edges: ON + OW) by age class and month for the Bay of Biscay anchovy. Age-1 is shown either including the new semihyaline edges (opaque edges + OH2), which occur during summer time, or excluding them (opaque = ON + OW). New semihyaline edges (OH2) refer to the transition edges from opaque to hyaline that is not entirely visible around the entire margin of the otolith that appears after having resumed (or completed) the annual marginal opaque growth.

DEPM survey ( $n = 20$ ) were 0.435 ( $P = 0.055$ ) and 0.677 ( $P = 0.001$ ) respectively, whereas for the acoustics survey ( $n = 14$ ) these correlations were 0.819 ( $P = 0.0003$ ) and 0.509 ( $P = 0.063$ ) respectively.

Two additional indirect historical validations of the age determination were achieved with surveys. First, a significant linear relationship was found between the ratio of biomasses in two consecutive years of the spring surveys and the odds ratio for age-1 in the second year ( $r = 0.722$ ,  $P < 0.0000$ ,  $n = 37$ ; Fig. 7a). This implies that globally the surveys were properly tracking the biomass oscillations of the anchovy population and that the age readings of age-1 and age-2+ were globally accurate. Second, a significant linear relationship was found between the abundance of juvenile anchovies (age-0) estimated by the JUVENA acoustic survey series in autumn and the estimates of recruits at age-1 in either of the two spring surveys of the following year (for the DEPM survey,  $r = 0.955$  and  $P < 1.6 \times 10^{-5}$ ; for the acoustic survey,  $r = 0.931$ ,  $P < 9.1 \times 10^{-5}$ ; 10 observations in each; Fig. 7b). This implied both that surveys were consistently estimating

the biomass of recruits and that age-0 and age-1 groups were well identified from otoliths.

#### Annual growth pattern in length and growth parameters

There were no major trends in the series of mean length at age in catches of the Spanish spring fishery (see the series and arithmetic mean values in Fig. 8a). However, mean lengths at age in catches were larger than those measured by the direct surveys of the population in May as part of the DEPM survey (Fig. 8c). In recent years, there has been a slight declining trend in the population mean length at age estimated by the DEPM survey (significant for age-1 and age-2; Fig. 8c). The VBGF curves are shown in Fig. 8b, d, and the parameters are given in Table 2.

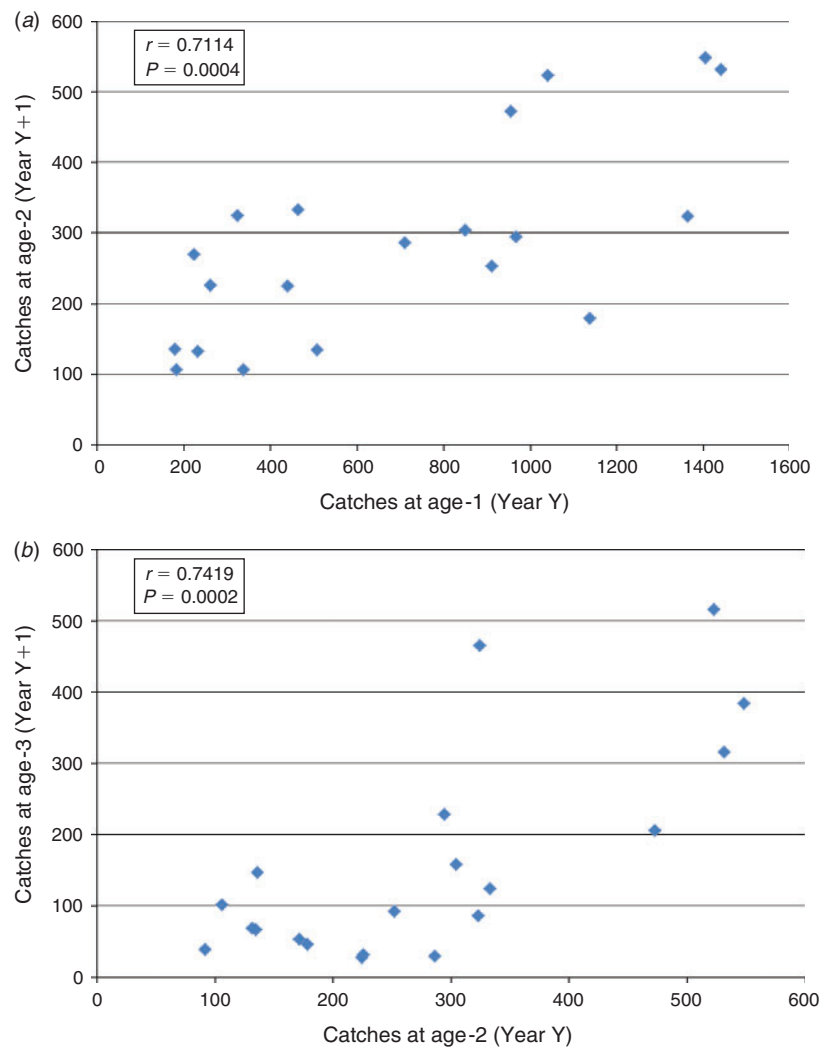
## Discussion

### Validation methods

Our validation was successful in applying the method of tracking strong year-classes, particularly for that of 1982 in the spring Spanish fishery (Fig. 2). Certainly, the moderate fishing effort at the beginning of the study and the occurrence of a strong (1982) cohort, followed by several medium or weak year-class, allowed us to track the 1982 year class up to the age of 5. Previously, Uriarte and Astudillo (1987) reported similar progressions of modal lengths in catches in this fishery, also indicative of the passing of spasmodic strong year classes. However, in 1987 the fishing effort increased with the addition of the French pelagic fishery and subsequently individuals of age-3+ became scarcer. Monitoring of the progression of strong year-classes in the catches afterwards would have been more difficult. For example, the 1989 strong cohort was only followed-up to the age of 3. Since then, many cohorts have disappeared after age-3: of the 19 cohorts from 1986 to 2004, only eight cohorts were seen at age-4).

The early detection of the 1989 year class in the catches of the second half of 1989 (at age-0) and the monitoring during 1990 and 1991 up to age-2 (Fig. 3) validated that Type I otoliths correspond to age-1. In addition, the combination of the study of the 1984 and 1989 year classes in catches with direct monitoring of several year classes between 1987 and 1992 in surveys concluded the validation procedure, because the strong increases in the population between years ought to be due to sharp increases in populations at age-1 (with Type I otoliths), as was, in fact, found by the surveys. The use of microstructure analysis by Aldanondo *et al.* (2016) has added a new validation of the first annulus deposition for this anchovy. Finally, our former validation of yearly growth patterns was confirmed and complemented with the monitoring of the occurrence of edge types throughout the year (Fig. 5).

Using surveys to support the validation of the ageing method is particularly suitable for short-lived species because the typical strong fluctuations in recruitment (which constitute the major part of the population) should result in rather parallel biomass fluctuations, provided that no major catchability problems affect the surveys. Therefore, age composition should support the interpretation of the biomass fluctuations being caused by recruitment fluctuations. For short-lived species for which there are ageing difficulties, but for which routine surveys of the



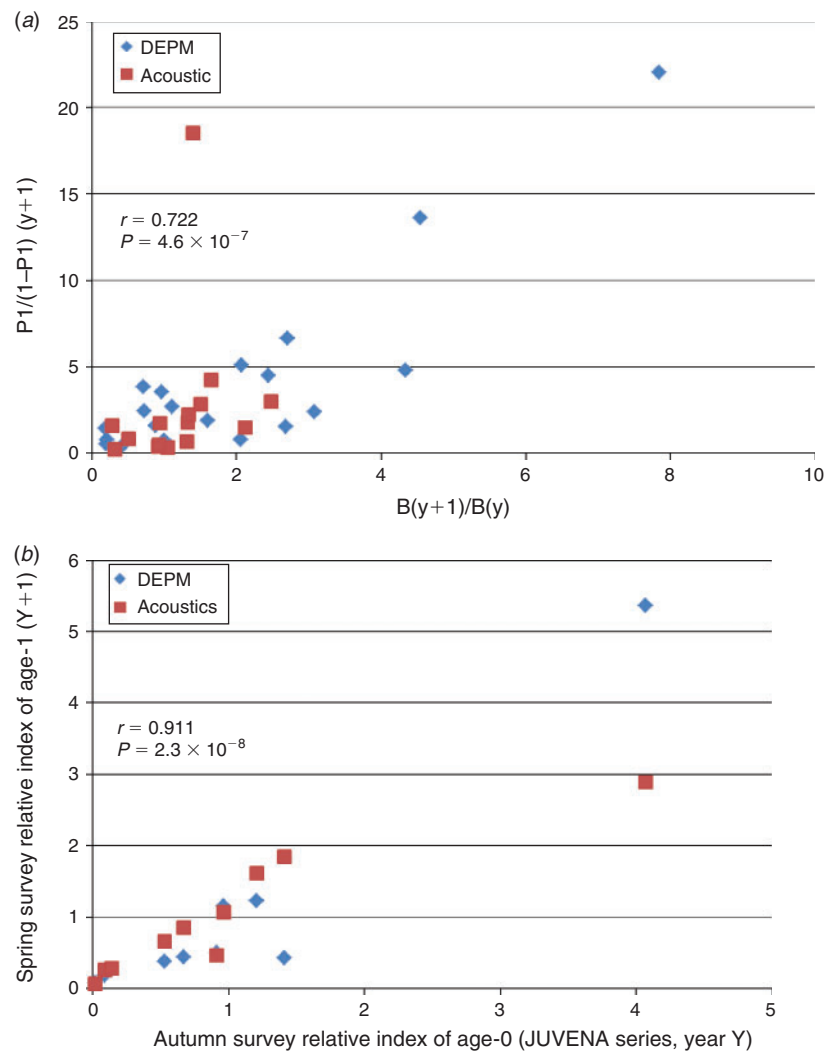
**Fig. 6.** Covariation of successive age groups in the catches in numbers ( $\times 10^6$ ) of the international fishery for (a) age-1 v. age-2 and (b) age-2 v. age-3.

population are conducted, the validation method described herein could be used to compare different ageing procedures. We used the method based on surveys to validate our initial ageing procedure and, subsequently, to corroborate the historical performance of the application of such an ageing method. The corroboration was expanded to the cross-correlation between the abundance of juvenile (age-0) and subsequent age-1 adults in surveys performed in autumn and spring respectively. This emphasises the considerable potential support of surveys when dealing with age validation problems for short-lived species.

The historical corroboration presented herein, making use of the whole series of age structures of catches and population estimates, was dependent, in part, on the precision and accuracy of the age determinations, as well as on the variability of the yearly catchability of the fishery and surveys (plus natural mortality). The overall level of precision in workshops on age determination is high, particularly for age-0 and age-1 (with agreements  $>93\%$ , CVs  $<10\%$  and negligible bias) but a bit

poorer for older ages (ICES 2009). However, for correlations between successive age groups of the same year class in catches to be significant, a rather constant fishing mortality at age (and hence fishing effort, as well as catchability and selectivity at age) between successive years and throughout the series is required so that the proportionality between catches of successive age groups remains relatively constant throughout the time series. However, the fishing mortality as a result of the fishery is known to have changed considerably since 1987 (ICES 2014), and is probably subject to yearly variability. In support of the latter, it is worth noting that the CV of the historical series of catches of the Spanish purse seine fishery is far lower than the CV of survey biomass estimates since 1987. For this reason we suspect that a major part of the wide variability found in Fig. 6, between pairs of catches of successive age groups of the same year classes, is probably due to yearly changes in effective fishing mortality beyond any inherent errors in the age determination. In addition, the fact that this relationship was no longer significant for the Spanish purse seine fishery when the last





**Fig. 7.** (a) Covariation of the ratio of successive biomass estimates in the spring daily egg production method (DEPM) surveys and acoustic survey series and the odds ratio of the proportion at age-1 in mass (P1) in every second year of the respective survey series. (b) Abundance of juvenile anchovies (age-0) in the JUVENA acoustic survey series in autumn (in any year Y) v. the estimates of recruits at age-1 in the spring of the following year (Y+1) in the DEPM and acoustic surveys.

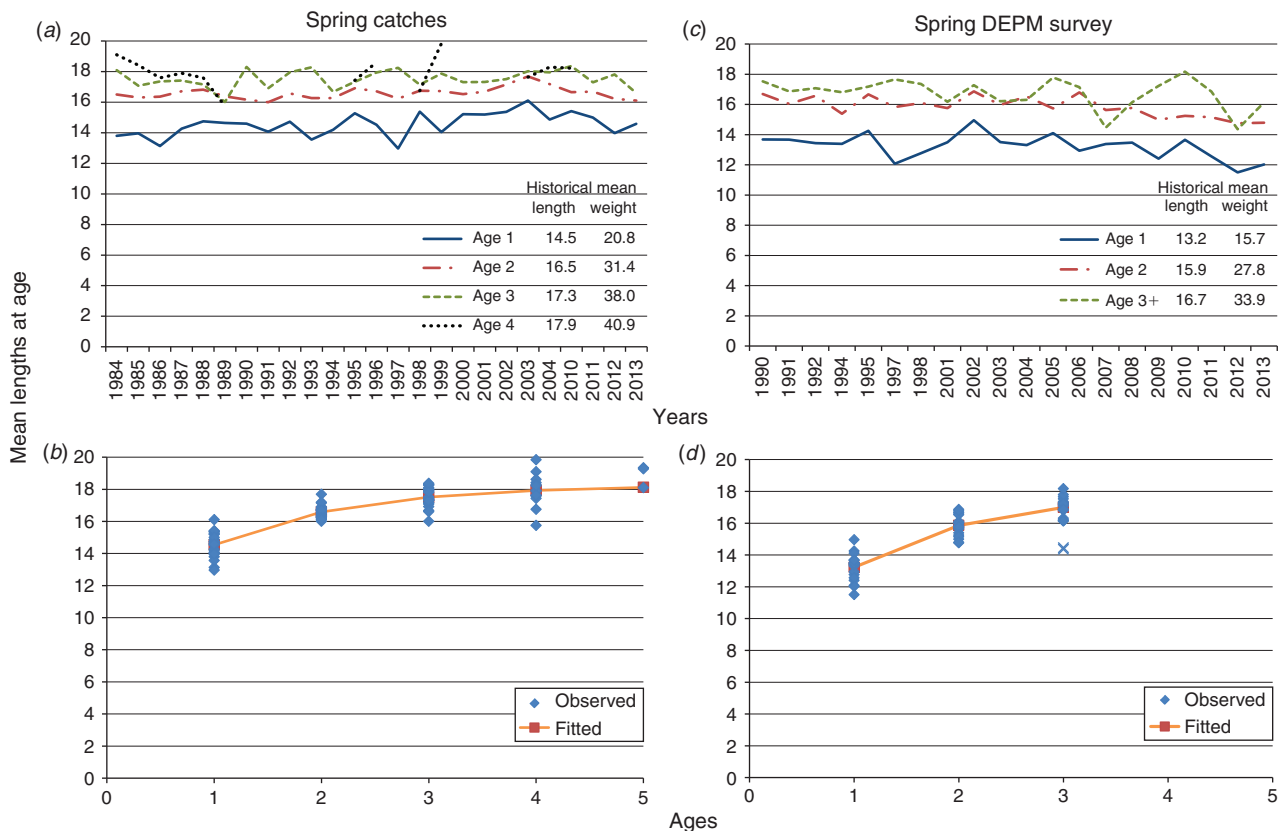
4 years were added likely indicates an intense change in fishing mortality in recent years as a result of the strong drop in fishing effort and a reduction in the fisheries during the first quarter and second half of the year as a result of the implementation of a management plan (ICES 2014). This may result in a higher survival at age-2 than before the closure of the fishery, leading to the abnormally higher catch rates of age-2 over age-1 individuals in recent years.

In parallel, the proportionality (linearity) of the abundance of successive age groups of the same year classes relies on the assumption of constant catchabilities at age at the time of the surveys. Although this constancy is presumed, the existence of occasional strong yearly catchability phenomena is also acknowledged in all surveys series, as revealed by the occasional strong divergence in the series of the two spring surveys

(ICES 2014). Therefore, a considerable part of the wide variability between the abundance of juveniles in autumn and age-1 individuals the following spring, or in the relationship between relative changes in successive spring biomass estimates and the odds of the proportion of individuals of age-1 in the second year (Fig. 7), must be due to random realisation errors in yearly catchability.

Finally, in addition to the former considerations, variability in natural mortality may introduce process errors in the correlation between catches or in the abundance of successive age groups of the same year-class.

Therefore, the corroboration methods used in the present study are rough approaches that are subject to quite a few observational and process errors. The fact that all the relationships turned out to be significant proved both that the age



**Fig. 8.** Anchovy length at age in the catches of the Spanish spring fishery 1984–2013 (a, b) and in the spring daily egg production method (DEPM) surveys 1990–2013 (c, d). (a, c) Mean length at age series and (b, d) von Bertalanffy growth curves fitted to the mean length at age. 'X' indicates abnormal mean length at age-3 that was omitted from the von Bertalanffy growth curves fitting. Historical mean length (cm) and weight (g) at age are given within (a) and (c).

readings were globally accurate and that observational and process errors affecting those relationships were not strong enough to mask the expected relationships.

#### Growth pattern of otoliths and age determination criteria

The validations demonstrated that annuli consist of a translucent zone (either a single or composite zone) plus a wider opaque zone, disrupted occasionally by some typical checks. The otolith growth is intense until the end of the second year of life (i.e. for the first 18–20 months), whereby opaque growth at age-1 is still substantial: ~50% that at age-0. As such, most otoliths are the result of growth periods at age-0 and age-1, with the growth at age-0 alone usually accounting for the major part of the otolith. Otolith increments at age-2 and older become gradually and steadily narrower. In this way, the general principle by which year growth increments gradually decrease (Morales-Nin and Panfili 2002) is obeyed, but the particular way in which otoliths grow in this anchovy is the first general scheme age readers should be aware of for the examination of these otoliths.

In addition to this general otolith growth pattern, there is large individual variability in the size of annual opaque growth increments by age. Much of this variability is due to the inverse relationship between the growth achieved during the first year of life (at age-0 until the first hyaline annulus) and the second and third years of life (at age-1 and age-2), as noted by Petitgas and

Grellier (2003) and in the quantitative analysis presented in the second section in the Supplementary material. This is indicative of the compensatory growth (the smaller fish tend to catch up with larger ones), which is observed in other marine species, also as a result of following the von Bertalanffy model or similar growth patterns (Taylor 1962; Ricker 1975; Xiao 1994).

#### Seasonal otolith growth pattern

Generally, the maximum occurrence of the translucent zone for all ages corresponded to the period of coldest sea temperature in late winter, whereas the maximum occurrence of opaque growth edges occurred with increasing temperatures during late spring and summer. This is typical for fish species at mid latitudes (Beckman and Wilson 1995; Cappo *et al.* 2000), including several small pelagic species, such as the Tunisian anchovy (Khemiri *et al.* 2007), Californian anchovy (Mallicote and Parrish 1981) and tapertail anchovy (He *et al.* 2008). However, the seasonal development of the marginal growth of otoliths differs between ages, with young anchovy (1 year old) resuming opaque growth earlier (from March) than older anchovy, which resume growth in late spring or early summer. This tendency for the younger fish to resume growth earlier than older fish was first noted for this anchovy by Guerault and Avrilla (1974), and it seems to be a widespread feature (Williams and Bedford 1974; Holden and Raitt 1974), also affecting clupeids such as

**Table 2. Growth of the Bay of Biscay anchovy (*Engraulis encrasicolus*) compared with other anchovies of the same genus: von Bertalanffy growth (VBG) function parameters and respective estimation of length at ages 1–4**

‘Source’ refers to the reference where the parameters came from. All works were based on otolith examination, except for those indicated as ‘LBA’ (length-based analysis). SST, sea surface temperature;  $\phi'$ , Pauly and Munro (1984) growth index; TL, total length; FL, fork length; SL, standard length;  $L_{\infty}$ , ratio of the mean length at age-1 over theoretical maximum length ( $L_{\infty}$ ); K, growth coefficient;  $t_0$ , theoretical age at length = 0

Scientific name	Geographic region		Annual mean SST (°C)	Length	VBG parameters				Mean length at age (cm)				$L_1/L_{\infty}$ (%)	Source	
	Area	Latitude			$L_{\infty}$	K	$t_0$	$\phi'$	Age-1	Age-2	Age-3	Age-4			Mean (1+2)
<i>E. encrasicolus</i>	North Sea	51°N	12.0	TL	20.59	1.14	0.1	2.68	14.6	18.7	20.0	20.4	16.6	71	Blaszczyk (1999)
<i>E. encrasicolus</i>	Bay of Biscay	44°N	16.0	TL	18.28	0.79	1.00	2.42	14.5	16.6	17.5	17.9	15.6	80	Present study (catches)
<i>E. encrasicolus</i>	Bay of Biscay	44°N	16.0	TL	17.85	0.85	0.60	2.43	13.3	15.9	17.0	17.5	14.6	74	Present study (surveys)
<i>E. encrasicolus</i>	Bay of Biscay	44°N	16.0	TL	17.25	0.92	1.05	2.44	14.6	16.2	16.8	17.1	15.4	85	Hernández <i>et al.</i> (2009)
<i>E. encrasicolus</i>	Bay of Biscay	44°N	16.0	TL	24.33	0.33	0.7	2.29	10.4	14.3	17.2	19.2	12.4	43	Cendrero <i>et al.</i> (1981)
<i>E. encrasicolus</i>	Bay of Biscay	44°N	16.0	TL	22.10	0.54	0.1	2.42	9.8	15.0	17.9	19.7	12.4	44	Gueraut and Avrilla (1974)
<i>E. encrasicolus</i>	Cadiz (Spain)	36°N	18.5	TL	18.69	0.89	0.02	2.49	11.1	15.6	17.4	18.2	13.4	60	Bellido <i>et al.</i> (2000) (LBA)
<i>E. encrasicolus</i>	NW Mediterranean	41°N	18.6	TL	18.19	0.45	1.09	2.17	11.1	13.6	15.3	16.3	12.4	61	Pertierra (1987)
<i>E. encrasicolus</i>	NW Mediterranean	41°N	18.6	TL	20.60	0.38	0.94	2.21	10.7	13.9	16.0	17.4	12.3	52	Pertierra (1987)
<i>E. encrasicolus</i>	NW Mediterranean	41°N	18.6	TL	19.10	0.35	1.45	2.11	11.0	13.4	15.1	16.3	12.2	57	Morales-Nin and Pertierra (1990)
<i>E. encrasicolus</i>	Sicilian waters	37°N	19.2	TL	18.60	0.29	1.81	2.00	10.4	12.4	14.0	15.2	11.4	56	Basilone <i>et al.</i> (2004)
<i>E. encrasicolus</i>	Adriatic Sea	42°N	17.6	TL	19.40	0.57	0.50	2.33	11.1	14.7	16.8	17.9	12.9	57	Sinović (2000)
<i>E. encrasicolus</i>	Adriatic Sea	42°N	17.6	TL	16.15	0.40	2.04	2.02	11.4	12.9	14.0	14.7	12.1	70	Arneri <i>et al.</i> (2011)
<i>E. encrasicolus</i>	Aegean and Ionian seas	38°N	18.0	TL	17.50	0.51	0.89	2.19	10.8	13.5	15.1	16.0	12.1	62	Machias <i>et al.</i> (2000)
<i>E. encrasicolus</i>	Black Sea	44°N	20.0	TL	19.10	0.35	1.45	2.11	11.0	13.4	15.1	16.3	12.2	57	Karacam and Düzgünes (1990)
<i>E. encrasicolus</i>	Black Sea	44°N	20.0	TL	16.77	0.32	2.07	1.96	10.5	12.3	13.5	14.4	11.4	63	Erkoyuncu and Ozdamar (1989)
<i>E. encrasicolus</i>	Tunisian waters	37°N	19.0	FL	19.16	0.32	1.68	2.07	11.1	13.3	14.9	16.1	12.2	58	Khemiri <i>et al.</i> (2007)
<i>E. encrasicolus</i>	Tunisian waters	34°N	19.0	FL	17.19	0.36	1.01	2.03	8.9	11.4	13.1	14.4	10.1	51	Khemiri <i>et al.</i> (2007)
<i>E. encrasicolus</i> <sup>A</sup>	SW African waters	33°S	16.9	FL	12.10	0.97	1.32	2.15	10.8	11.6	11.9	12.0	11.2	89	Melo (1984)
<i>E. encrasicolus</i> <sup>A</sup>	SW African waters	33°S	16.9	FL	13.00	1.33	0.17	2.35	10.2	12.3	12.8	12.9	11.3	79	Melo (1984)
<i>E. encrasicolus</i> <sup>A</sup>	SW African waters	33°S	16.9	FL	14.00	1.49	0.00	2.47	10.8	13.3	13.8	14.0	12.1	77	Melo (1984)
<i>E. mordax</i> <sup>B</sup>	Peru (central)	12°S	18.0	TL	20.49	0.88	0.00	2.57	12.0	17.0	19.0	19.9	14.5	58	Palomares <i>et al.</i> (1987)
<i>E. mordax</i> <sup>B</sup>	Peru (south)	17°S	16.0	TL	17.50	1.40	0.18	2.63	14.2	16.7	17.3	17.4	15.4	81	Morales-Nin (1989)
<i>E. mordax</i> <sup>B</sup>	Chile	19°S	16.0	TL	19.04	0.73	0.02	2.42	10.0	14.7	16.9	18.0	12.3	52	Aguiayo (1976)
<i>E. mordax</i> <sup>B</sup>	Chile	25–33°S	15.5	TL	19.50	0.55	1.00	2.32	13.0	15.7	17.3	18.2	14.3	66	Canales and Leal (2009)
<i>E. mordax</i> <sup>B</sup>	Chile	37°S	12.5	TL	20.80	0.51	0.04	2.35	8.6	13.5	16.4	18.2	11.1	41	Cubillos <i>et al.</i> (2001) (LBA)
<i>E. mordax</i>	California	37°N	15.0	SL	16.56	0.30	1.71	1.91	9.2	11.1	12.5	13.6	10.2	56	Spratt (1975)
<i>E. anchoita</i>	Argentina/Uruguay	35°S	16.4	TL	17.30	0.71	0.9	2.33	12.7	15.1	16.2	16.8	13.9	74	Brandhorst <i>et al.</i> (1974)
<i>E. japonicus</i>	Yellow Sea, China	35°N	20.0	TL	15.50	0.60	1.0	2.16	10.8	12.9	14.1	14.7	11.9	70	Iverson <i>et al.</i> (1993)

<sup>A</sup>Formerly *E. capensis*.

<sup>B</sup>Formerly *E. rigens*.

the Baltic sprat, herring and Atlantic sardine (ICES 2008a, 2008b, 2011). Because most of the expected annual opaque increment of the otoliths is completed for all ages by the end of September, otolith growth for the 1-year-old fish occurs from March to September (in ~7 months), whereas otolith growth for fish aged 2 and 3 years old occurs from June and July to September (i.e. in ~4 and 3 months respectively). As such, there is some parallelism between the decreasing gain in length by age and the decreasing time of opaque growth formation in otoliths by ages.

Understanding the seasonal development of the marginal edge by ages was relevant to improving the accuracy of age determination, particularly discriminating age-1 from older fish during spring, when most of the 1-year-old fish will show an opaque narrow edge type whereas older fish are still laying down hyaline edges. For this reason, it could be worth considering this issue further to improve age determination procedures in small short-lived pelagic fishes of other areas too.

### Checks

Many fish species lay down checks in their otoliths associated with non-periodic stress, such as environmental conditions (storms, cooling, starvation), life history transitions, endogenous processes (hatching, maturation, spawning) or cyclic environmental issues (Pannella 1971; Campana and Neilson 1985; Casselman 1987). The incidence of checks is particularly common in young fish (from age-0 to age-2) of many species (Swan and Gordon 2001; Waldron and Kerstan 2001; Santiago and Arrizabalaga 2005), including pelagics (Thomas 1983, 1984), and hence probably affects the predominant age group of short-lived species. Therefore, our observations of several checks in this anchovy were not surprising. Fortunately, they are recurrent and become typically identifiable, so that readers can become familiar with them.

The earliest checks are formed in autumn (October–December) when anchovy juveniles move from the surface waters over wide regions of the Bay of Biscay to deeper and more coastal waters where they overwinter (Uriarte *et al.* 2001; Irigoien *et al.* 2007). This change may induce a first check, associated with either a change in water temperature or temporary poor feeding conditions. This possibility has been supported by the bioenergetics modelling of otolith biomineralisation for this anchovy by Pecquerie *et al.* (2012), who were able to simulate check formation in the age-0 group of anchovies by simulating poor feeding conditions before winter. These types of checks before the first annulus have also been reported in south-west African pilchard and anchovy (Thomas 1983; Melo 1984) and in the Chilean anchovy (Aguayo 1976).

Later, during winter, split rings can occur, especially in fast-growing age-0 fish, where the translucent zone is interrupted by one or two short periods with opaque growth if food and temperature conditions are good. These split rings are commonly associated with the first translucent zone of many fish species (Panfili *et al.* 2002; Santiago and Arrizabalaga 2005) and have also been reported for pilchard off south-west Africa (Thomas 1983, 1984).

The most common check is observed in age-1 fish from July onwards, but is formed in the middle of the second opaque zone in June during the peak spawning time of the 1-year-old

anchovies (Motos 1996). In older fish, maturation and peak spawning is earlier, and the opaque growth of the otolith does not resume before spawning, but rather mainly in June–July. This check could be a spawning check laid down by the fast-growing 1-year-old anchovy after its initial opaque growth during spring, whereas older anchovies may be merging the hyaline winter annulus with the spawning check (resulting in the widening of the hyaline zone during spring). This probably reflects the different relative investment of energy in growth and reproduction of the younger *v.* older anchovies, with the former investing relatively more in growth whereas the latter invest more in reproduction (as also suggested by the dynamic energy budget modelling of this anchovy; Pecquerie *et al.* 2009). Spawning checks are reported to occur in many fish (Casselman 1987), including South African anchovy (Melo 1984; Waldron 1994) and Chilean anchovy (Aguayo 1976). In addition, a similar check within the opaque growth of the second year of life (age-1) has been reported for Pacific anchovy (Collins and Spratt 1969) and Mediterranean anchovy (Pertierra 1987). In some cases, if spawning is close to winter, a composite hyaline zone may be formed of the spawning check plus the winter annulus, or it can be merged in older fish, as seems to happen for the Bay of Biscay anchovy and for the south-west African pilchard (Thomas 1983, 1984) and other fish (Casselman 1987; Hsu and Tzeng 2009).

The present study corroborated that false checks are not equally laid down in all fish or in all year classes, as reported for other species too (Thomas 1983, 1984; Campana and Neilson 1985; Casselman 1987). This irregular incidence impeded the formulation of a simple rule based purely on the counting of every hyaline zone.

### Annual growth patterns in length and growth parameters

Since the current methodology was applied in the late 1980s, the mean lengths at age have remained almost constant throughout the time series in the catches of the spring Spanish fishery, with von Bertalanffy growth parameters similar to those calculated by Hernández *et al.* (2009), also for the Spanish fishery, and Vaz *et al.* (2002) for the acoustic surveys in the Bay of Biscay. However, these results are in contrast with those published previously by Cendrero *et al.* (1981) for the Spanish fishery and by Guerault and Avrilla (1974) in the French area, which reported length at age-1 of ~10 cm and length at age-2 of ~14.5 cm in catches (i.e. the latter corresponds to values obtained using the method described herein for mean length at age-1; Table 2). Furthermore, using the current procedure of age determination using otoliths resulted in a shift in the proportion of major age groups supporting the Spanish spring catches, by which age-1, which was formerly almost absent, became very abundant (Anon. 1993). The differences with the results reported by Cendrero *et al.* (1981) are probably due to the initial use by those authors of probabilistic techniques for the analysis of polymodal length–frequency distributions for several years (Cort *et al.* 1976) before the use of otoliths. In addition, there could also be some differences in ageing criteria. Conversely, the mean lengths at age calculated by Guerault and Avrilla (1974) were back-calculated at the time of translucent annulus formation; this, coupled with the fact that they were working on the French shelf close to shore (including the Gironde area,



where anchovies are usually smaller), may explain the differences in results.

The present study evidenced lower mean lengths at age (and weights) in the population (as estimates from the DEPM surveys) than in the catches of the concurrent spring Spanish fishery, so that they resulted in a slightly higher growth coefficient ( $K$ ) and lower theoretical maximum length ( $L_{\infty}$ ) (Table 2). The reason for these differences is related to the spatial pattern of the Spanish fishery because it operates in regions of deep water rather close to the Spanish coast where the bigger anchovies are found (Uriarte *et al.* 1996; Ibaibarriaga *et al.* 2013). In contrast, the surveys systematically cover all areas occupied by the population, with the major part of the population often placed around the northern coastal shelf close to the mouth of the Gironde River where age-1 predominates and the mean lengths at ages are smaller than in the remaining areas (Motos *et al.* 1996; Vaz *et al.* 2002; Ibaibarriaga *et al.* 2013).

This anchovy population has an intense growth rate compared with other populations of the same species or with other Engraulidae (Table 2). The rather high  $L_{\infty}$  and  $K$  values result in it having among the highest  $\phi'$  parameter of this genus, only equalled or surpassed by anchovies in the North Sea and by anchovies in Cadiz. However, looking at the mean of lengths at age-1 and age-2, only *E. encrasicolus* in the North Sea seem to be bigger (Błaszczuk 1999); however, a more recent comparison with otoliths from the International Bottom Trawl Surveys in the North Sea along the Dutch coast shows rather comparable mean lengths at age (Petitgas *et al.* 2012). Despite several populations having similar or higher  $L_{\infty}$  in the Mediterranean, the low  $K$  means they have smaller mean lengths at ages 1 and 2 and lower  $\phi'$ . So, the average size and growth of these populations are smaller. *E. encrasicolus* of South Africa has a higher  $K$  but smaller  $L_{\infty}$  so that despite its rather similar  $\phi'$ , mean sizes at age-1 and age-2 are also smaller. The Peruvian and northern Chilean anchovies are those that have rather similar growth rates and mean lengths at age-1 and age-2 (Aguayo 1976; Palomares *et al.* 1987; Morales-Nin 1989). Most other Engraulidae have smaller sizes at age-1 and age-2 regardless of their actual growth rates or  $\phi'$  (Hoedt 1990; Tiroba *et al.* 1990), except for the large tropical anchovy *Thryssa hamiltoni* (Hoedt 1992). Anchovies inhabiting estuarine areas also tend to be smaller (Iversen *et al.* 1993; Newberger and Houde 1995; He *et al.* 2008). Aldanondo *et al.* (2011), analysing micro-increments in the otoliths of juveniles, has shown that this anchovy in the Bay of Biscay can reach a size of 6–8 cm in ~70–90 days. All these observations reflect the life strategy of this short-lived anchovy, namely very intense growth during its first year of life so that it maximizes its size at the age of first maturity (i.e. at age-1 and, thus,  $L_1/L_{\infty}$ ) and hence the reproductive output of its first spawning season. This, coupled with a still substantial growth during its second year of life, should maximize the overall reproductive output across its expected life, because survivors at older ages become negligible.

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